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MORPHOLOGY AND POSTEMBRYONIC DEVELOPMENT OF *RHIZOGLYPHUS ECHINOPUS* (FUMOUCHE & ROBIN) (CHELICERATA, ACTINOTRICHIDA)

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With 12 text-figures

ABSTRACT

A study is made of the morphology and postembryonic development of *Rhizoglyphus echinopus* (Fumouze & Robin), a species of Acaridida (Actinotrichid mites). The study is based on the same methods and principles as the author's previous studies of mites and other groups of Chelicerates. Particular attention is paid to the homology of the setae of idiosoma and appendages, and to the postembryonic development of the paraproctal setae. A new interpretation is given of bursa copulatrix and fertilization.

Our knowledge of the morphology and postembryonic development of Acaridida (= Acarididae), as far as published until now, is not easily comparable with that of other groups of Actinotrichid mites. Detailed, more or less complete descriptions are nearly lacking, and conventions with reference to description, the orientation of illustrations, and the use of sigla (notations) are generally different from those used in modern studies of Actinedida, Oribatida and Tarsosomida. Grandjean (1937, 1937a, 1938, 1938a, 1939, 1953) published several papers of fundamental importance, dealing with podocephalic canal and podocephalic glands, genital region, suckers, leg segmentation and leg chaetotaxy, postembryonic development, and the relationships between Acaridida and other groups of Actinotrichid mites. He studied the leg chaetotaxy of Acaridida (Grandjean, 1939) before he had developed his general system of sigla for the use in Actinotrichid mites; later on (Grandjean, 1953: 392-393) he published some remarks on possible homologies. Although Grandjean's earlier system of notation was adopted by several specialists of Acaridida, his later remarks remained practically unobserved. Knülle (1958, 1959) studied the morphology and postembryonic development of Acaridida, with particular reference to *Acarus siro* L. He was the first to apply Grandjean's notation for the Actinotrichid notogastral and epimeral setae to Acaridida. He did not solve the pro-

blem concerning the homology of the tarsal setae, and his interpretation of the postembryonic development of the paraproctal setae is different from that introduced in the present paper. The postembryonic development of the idiosomatic setae was recently reinvestigated by Griffiths (1977); his results are discussed below (he did not apply Grandjean's system of notation).

The present study of the morphology and postembryonic development of Acaridida is based on *Rhizoglyphus echinopus* (Fumouze & Robin), of which an abundant material was at my disposal¹⁾. *Rhizoglyphus echinopus* is a free-living species, now generally classified with the family Acaridae. It does not present many highly specialized characters, and appeared to be excellently suited for the present study. Terminology and methods used in the present paper are based on the general part of the Glossary of Acarological Terminology (Van der Hammen, 1980), and are similar to those used in my previous comparative studies of mites and other groups of Chelicerates. The greater part of the present paper consists of a detailed description of *Rhizoglyphus echinopus*; this is followed by some general remarks.

***Rhizoglyphus echinopus* (Fumouze & Robin)**

Material. — Numerous specimens of the species, among which larvae, protonymphs, deutonymphs (hypopi), tritonymphs, adult females, and adult homomorphic and heteromorphic males, have been collected from bulbs (mainly hyacinth, but also narcissus and possibly other species of bulbs), originating from Lisse, The Netherlands. The bulbs were received in October 1968, when some *Rhizoglyphus* material was collected by hand; they were subsequently placed on a modified Berlese funnel (without electric bulb) where they remained until March 1969 (the collecting jars were regularly replaced). The material was already used by me to prepare the figures of adult female and hypopus for my short introduction to acarology (Van der Hammen, 1972: figs. 34, 35; these figures are reproduced, with sigla, as figs. 1 and 12 of the present paper). The material was used by Fain (1977) to prepare his description of the hypopus.

The identity of the material is based on the revision of the genus *Rhizoglyphus* by Van Eyndhoven (1961, 1968). The species was identified with *Rhizoglyphus callae* (Oudemans) by A. M. Hughes (1961: 78, fig. 96).

Measurements. — The measurements of the species are variable. For the present study one or a few specimens only of all stases have been measured. My data (in mm) are the following. Adult female: length 0.649-0.781, breadth 0.354-0.469. Adult homomorphic male: length 0.493, breadth 0.266. Larva: length 0.244, breadth 0.141. Protonymph: length 0.313, breadth 0.207. Deutonymph (hypopus): length 0.316-0.366, breadth 0.198-0.241. Tritonymph: length 0.354-0.443, breadth 0.186-0.245.

¹⁾ I am grateful to Mr. C. F. van de Bund, at that time attached to the Plant Protection Service, Wageningen, The Netherlands, who, on my request, supplied me with the material.

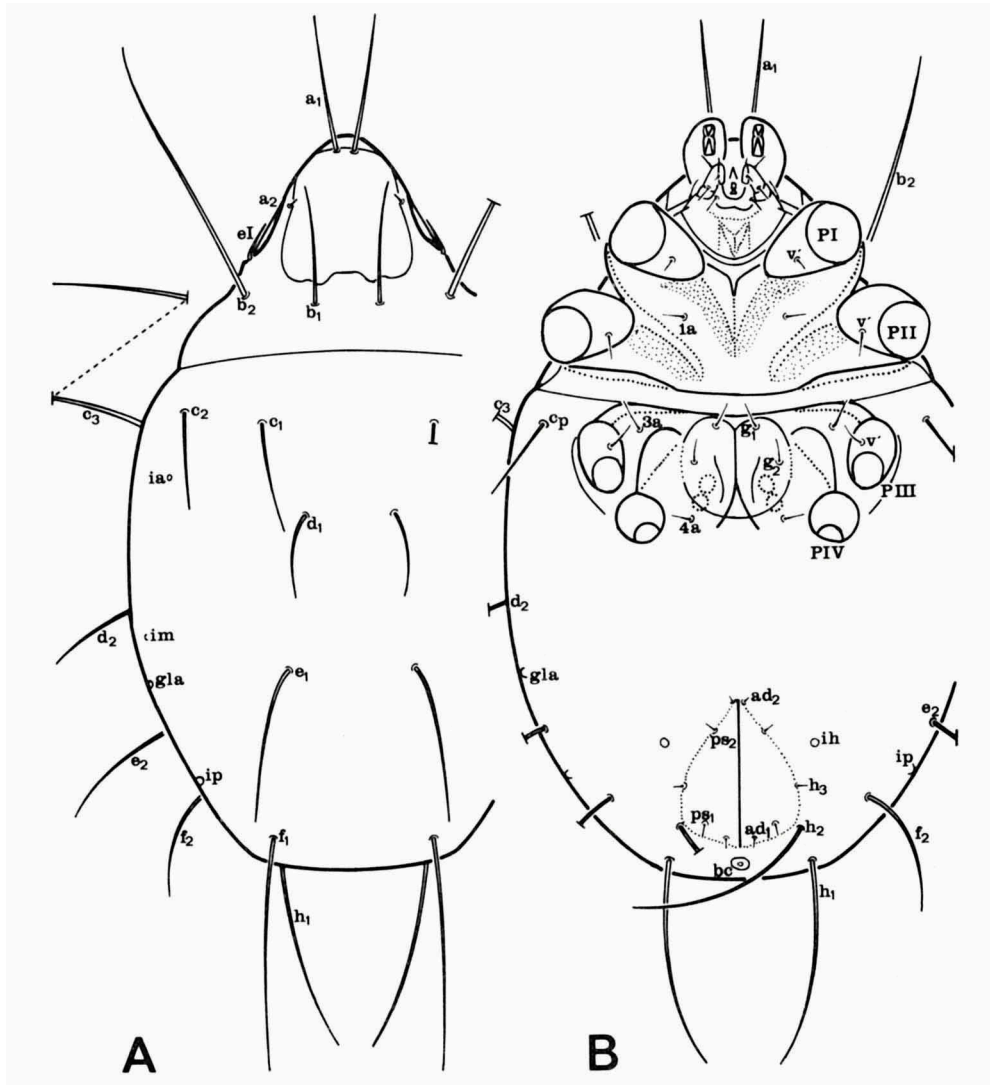


Fig. 1. *Rhizoglyphus echinopus* (Fumouze & Robin), adult female; A, dorsal view; B, ventral view; A, B, $\times 138$. (After Van der Hammen, 1972).

Divisions of the body. — The dorsodisjugal furrow separates the prodorsum from the opisthosoma (fig. 1A). The ventrosejugal furrow and interval separate the propodosoma from metapodosoma and opisthosoma (fig. 1B). Although both furrows are more or less in line with each other, they are not continuous (fig. 2). The gnathosoma is not protected by a rostral tectum (the species is astegasimous).

Tegument. — The cuticle is for the greater part soft and pale in colour; the cuticle of the appendages, and particularly of the chelicerae, is more distinctly sclerotized. There is a prodorsal sclerite (fig. 1A) in the anterior part of the aspidosoma. Sclerotization is more pronounced in the heteromorphic male.

Aspidosoma. — There are four pairs of prodorsal setae: a_1 (vertical internals), a_2 (vertical externals), b_1 (scapular internals) and b_2 (scapular externals); the new notation is introduced in order to match the notation of the notogastral setae (it is not possible to homologize the four pairs of prodorsal setae of Acaridida with some of the six pairs of prodorsal setae originally present in Oribatida and Actinedida).

Dorsal and laterodorsal aspects of opisthosoma. — The chaetotactic condition of this region is easily comparable with the condition in Oribatida and Actinedida. This is demonstrated by a study of the postembryonic development (which will be discussed below, in the paragraph in question). The (fused) opisthosomatic segments present in the adult are *VII/VIII(C)*, *IX(D)*, *X(E)*, *XI(F)*, *XII(H)*, *XIII(PS)* and *XIV(AD)*. The notation of the notogastral setae (figs. 1, 2), according to the system currently used in the study of Oribatida and Actinedida, is the following (the notations and the names of the setae currently used by specialists of Acaridida are added between brackets): c_1 (d_1 = dorsal 1st), c_2 (hi or l_1 = internal humeral or lateral 1st), c_3 (h = external humeral or humeral), c_p (hv or sh = ventral humeral or sub-humeral), d_1 (d_2 = dorsal 2nd), d_2 (la or l_2 = anterior or 1st lateral, or lateral 2nd), e_1 (d_3 = dorsal 3rd), e_2 (lp or l_3 = posterior or 2nd lateral, or lateral 3rd), f_1 (d_4 = dorsal 4th), f_2 (l_3 or l_4 = 3rd lateral or lateral 4th), h_1 (sai or d_5 = internal sacral or dorsal 5th), h_2 (sae or l_5 = external sacral or lateral 5th), h_3 , ps_1 , ps_2 (the adanal setae, together with the pseudanals, will be discussed in the paragraph on the paraproctal region; a comparative study of the notation of the h , ps and ad setae is made in the paragraph on the postembryonic development). There are four pairs of cupules (lyricupules): ia , im , ip and ih (cf. figs. 1, 2); ih is arranged on the same alignment as h_1 , h_2 and h_3 . The bursa copulatrix of the female, postero-dorsally of the anal opening, will be described in the paragraph on the genital region.

Paraproctal region. — The two paraproctal segments of *Rhizoglyphus* (and other Acaridida) are: the pseudanal segment ($PS = XIII$) and the adanal segment ($AD = XIV$). In female *Rhizoglyphus* these segments present two pairs of setae, the notation of which is: ps_1 , ps_2 , ad_1 , ad_2 . The pseudanal seta ps_3 , normally present in holotrichous Actinotrichida, is absent. In the adult male (fig. 4B) the adanal setae are replaced by a pair of suckers (homologized here with ad_1), whilst ps_1 has a more posterior position (on a transverse line with h_2). The pseudanal and adanal (lyri)cupules are not present (not discernable) in both sexes.

Genital region. — The longitudinal progenital opening is bordered by the progenital lips (figs. 1B, 3A). There are two pairs of progenital setae: g_1 (g_a or c_1 = anterior genital or first central) and g_2 (g_m or c_2 = median genital or second central). The eugenital opening (fig. 3A: og) is trifid. There are two pairs of genital papillae (Pg_a and Pg_p); they are situated (in rest) in cavities of the pro-



Fig. 2. *Rhizoglyphus echinopus* (Fumouze & Robin), adult female, lateral view; $\times 186$.

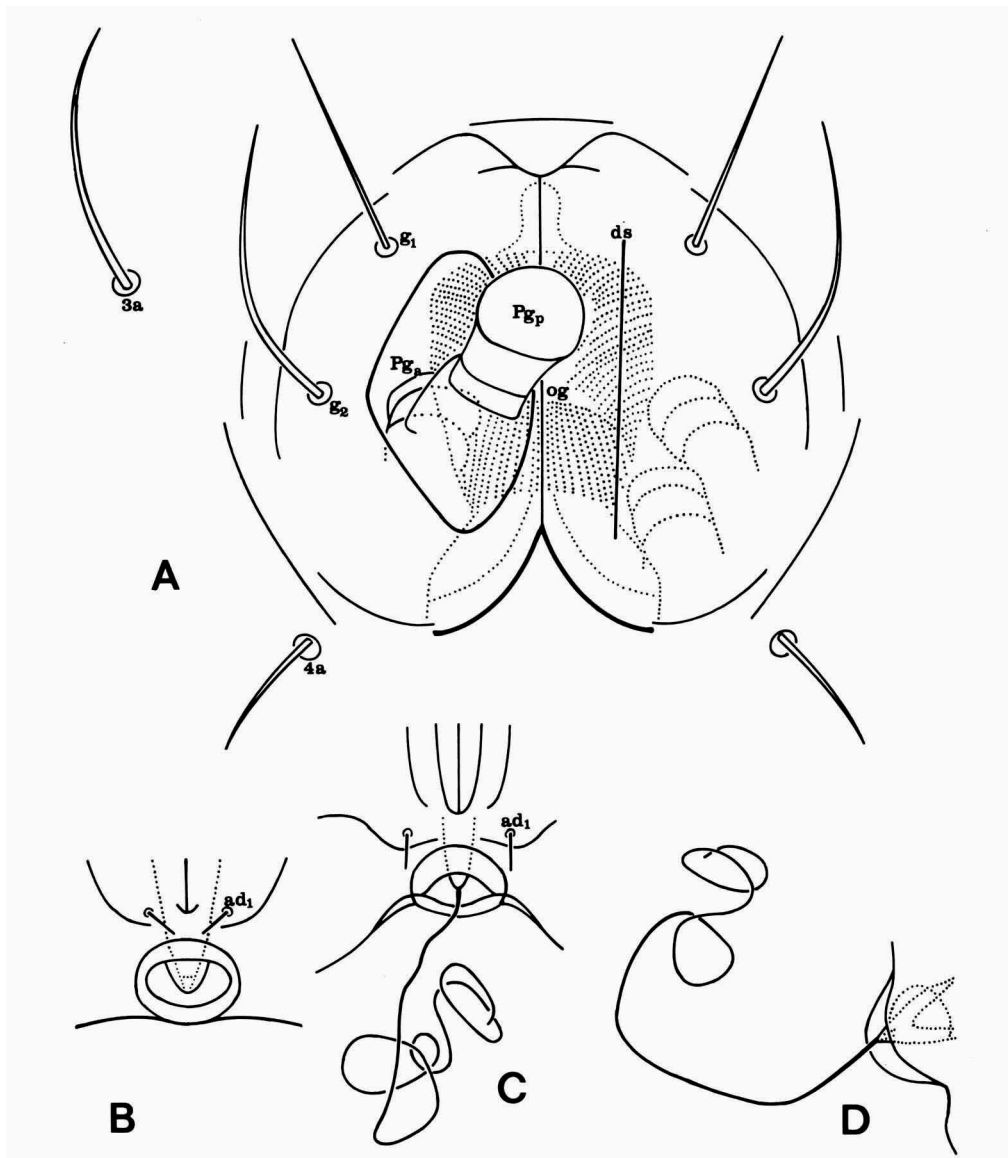


Fig. 3. *Rhizoglyphus echinopus* (Fumouze & Robin), adult female; A, ventral view of genital region; B-D, bursa copulatrix; B, ventral view; C-D, with extended sperm duct; C, ventral view; D, lateral view; A-D, $\times 687$.

genital lips, which open according to the so-called diachilous slit (*ds*). Grandjean (1938a: 284-285, fig. A-F) described the progenital lips as eugenital. The position of the eugenital opening (*og*) demonstrates that the posterior eugenital lip is indeed only partly covered by the progenital lips, but that the anterior pair of

eugenital lips is completely covered. This condition is a particular one, known from Acaridida only. It is now generally assumed that the bursa copulatrix of the female, situated posterodorsally of the anal opening (fig. 3B), has internal connections (by means of openings) with the ovaries. In one of my specimens (studied in lactic acid), of which I had just removed the legs, a long, narrow, chitinous duct (fig. 3C, D) was protruding; this duct was not visible in rest. It could represent the duct by which sperm, stored in the bursa copulatrix, is transported to the eugenital opening. The supposed internal openings to the ovaries could indeed represent the chitinous parts of glands (they are very similar to a type of unicellular gland with sclerotized collar at the place of junction between gland and duct). The male copulatory organ or penis (fig. 4B) is broad and rounded.

Epimeral region. — Epimera 1, 3, and 4 each present one seta (fig. 1B): 1a, 3a, and 4a, respectively (*CXI* or *s*, *CXIII* or *cx*₃, and *g*_p or *c*₃ in current literature on Acaridida). The genital opening has an advanced position between the pairs of epimera 3 and 4.

Lateral aspect of podosoma. — The podocephalic canal (figs. 2, 4A, C) extends from posterodorsally of leg I to the cervix (close to the line of attachment of the cheliceral frame to the infracapitulum). The canal is protected by a tectum of which the anterior part extends as Grandjean's organ (*GO*); the last-mentioned organ is bifurcate in *Rhizoglyphus echinopus*. The supracoxal seta *eI* of leg I is inserted close to the posterior part of the podocephalic canal; it is relatively large.

Gnathosoma. — The Acaridid gnathosoma consists (as in other Actinotrichida) of two parts: cheliceral frame and infracapitulum. The cheliceral frame extends from the rostral region of the aspidosoma to the infracapitulum. It is attached to the infracapitulum according to the line *at* (fig. 6A). The dorsal part constitutes the tegulum (fig. 6C: *TG*). The infracapitulum consists of a dorsal part (the cervix), a ventral part (mentum) and the malapophyses (with which the palps have partly fused). The cervix presents a median elevated part, named capitular saddle (fig. 6D: *se*). The internal continuation of the cervix is constituted by the capitular apodeme (fig. 6A: *ap.c*). Mentum and genae (the ventral region of the malapophyses) are continuous, not separated by an articulation. There is one pair of infracapitular setae, viz., the anterior pair *a* (belonging to the genae). There are three lips (figs. 5, 6A): the labrum (*LS*) and the pair of lateral lips (*LL*). The lateral lips have fused. There is, on either side of the base of the labrum, a distinct sclerotized thickening (the superior commissural induration), along the inner part of the superior commissural line, close to the superior oral commissure. As mentioned above, the palps have partly fused with the malapophyses. The malapophyses constitute the paired anterior region of the infracapitulum, in front of the base of the labrum and the base of the palp. The two terminal palpal segments are more or less free; they probably represent a genotibia and a tarsus. The tarsus presents the solenidion ω , a supposed vestige of a eupathidium, and one seta; the genotibia presents two setae (figs. 4C, 5, 6A). The supracoxal seta *e* is relatively large; in Actinotrichid mites, it is usually

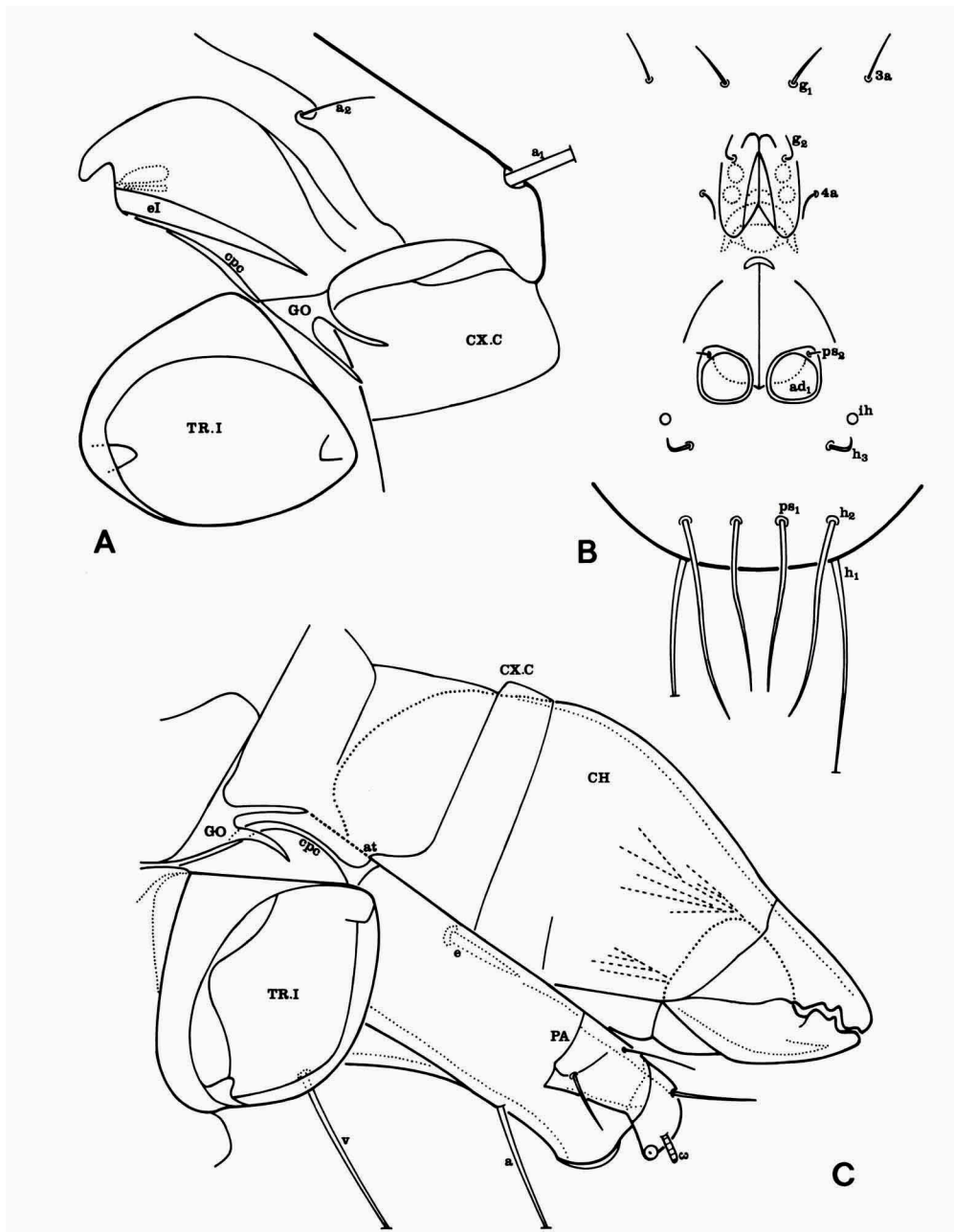


Fig. 4. *Rhizoglyphus echinopus* (Fumouze & Robin), A, region of podocephalic canal of adult female, lateral view; B, anogenital region of homomorphic male, ventral view; C, gnathosoma of adult female, lateral view; A, C, $\times 550$; B, $\times 186$.

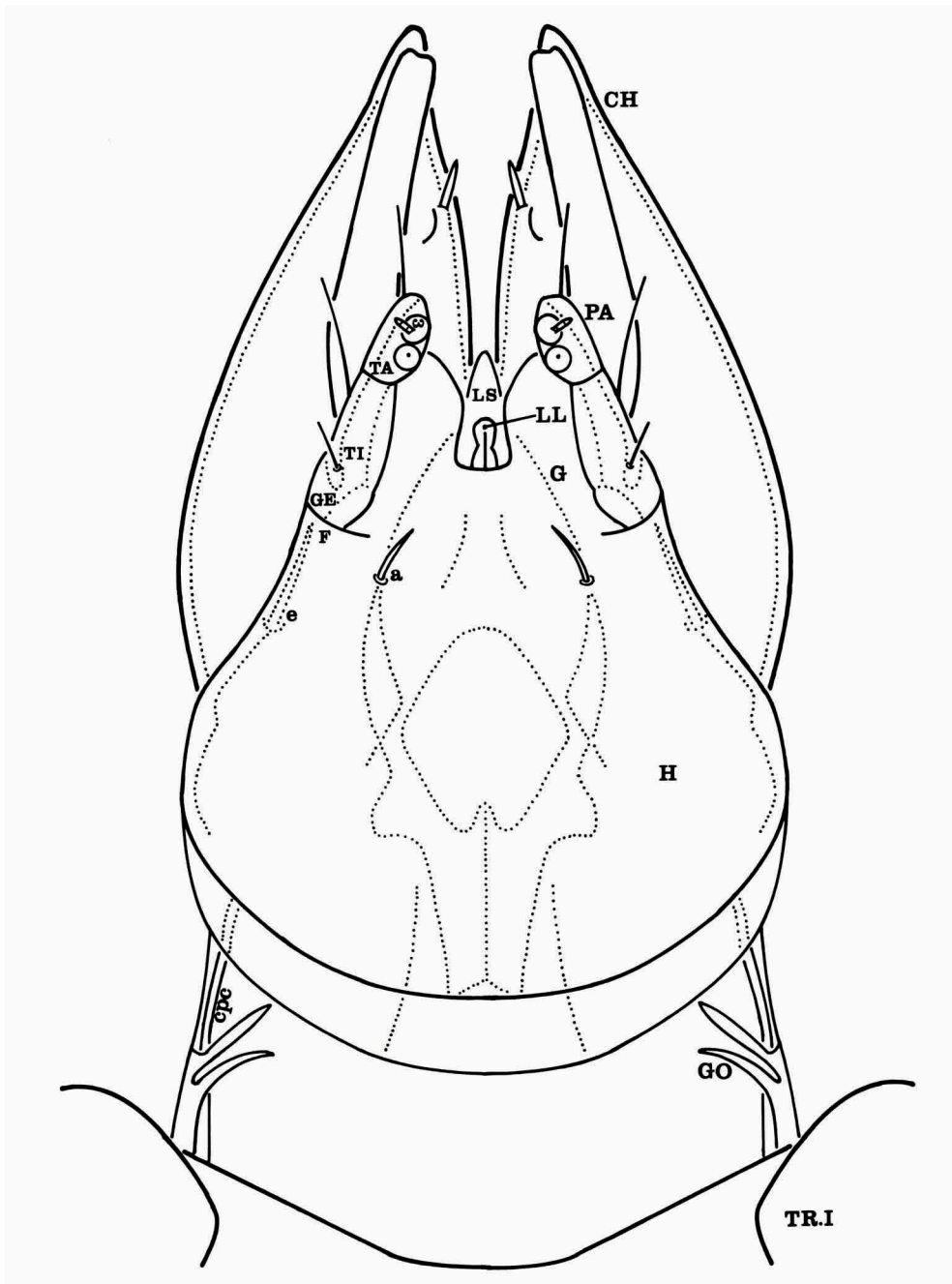


Fig. 5. *Rhizoglyphus echinopus* (Fumouze & Robin), gnathosoma of adult female, ventral view; $\times 825$.

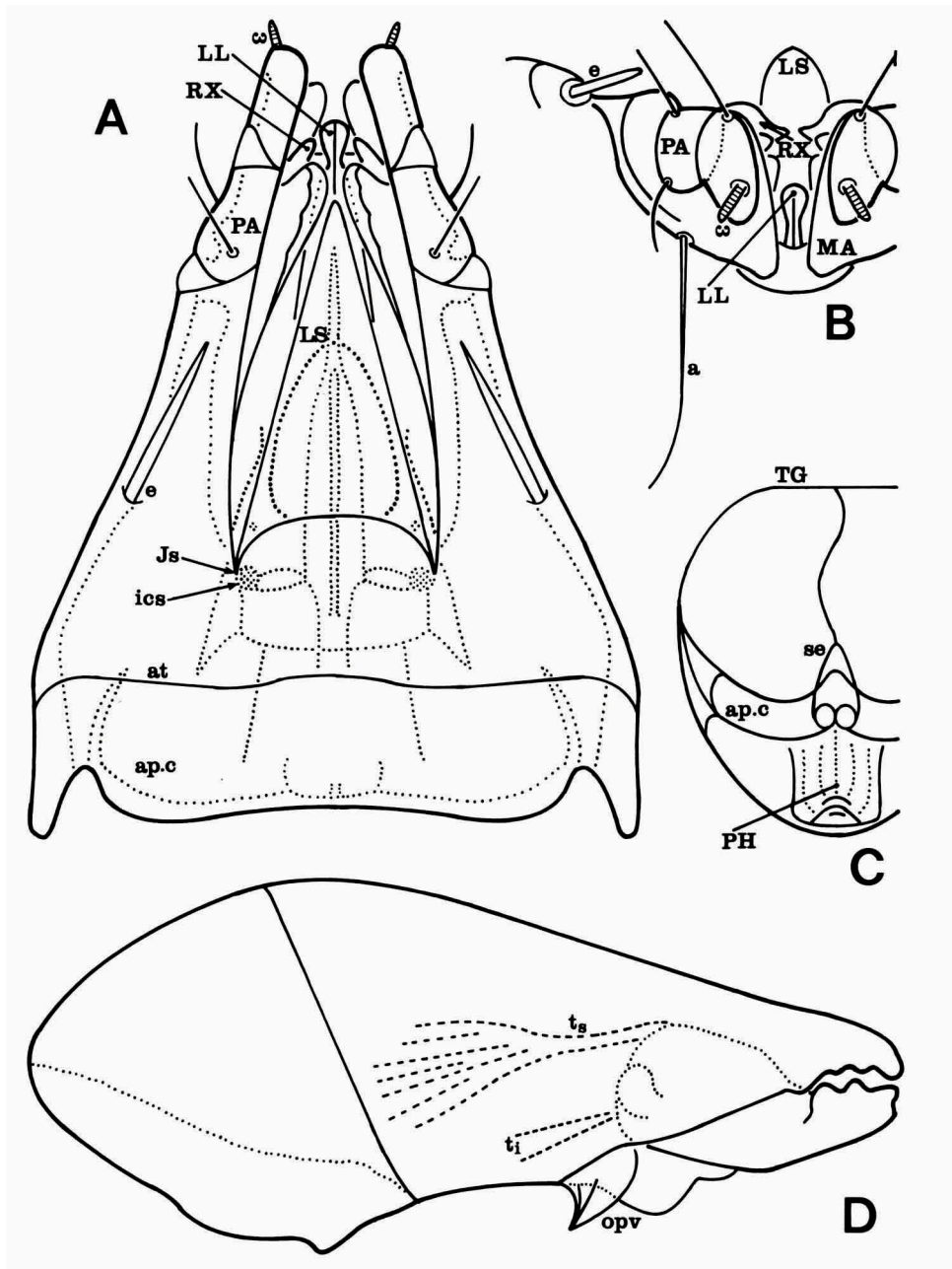


Fig. 6. *Rhizoglyphus echinopus* (Fumouze & Robin), adult female; A, B, infracapitulum; A, dorsal view; B, frontal view; C, gnathosoma, posterior view (chelicerae removed); D, right chelicera, lateral (antiaxial) view (orientation slightly oblique, in order to show the ventral oncofysis); A-B, D, $\times 825$; C, $\times 442$.

inserted above the base of the palp, and its position in *Rhizoglyphus* is an indication of the extension of the trochanterofemur, which is, on either side, completely incorporated into the malapophyses (figs. 4A, 5, 6A). On either side of the infracapitulum, mentum and cervix together constitute a large lateral ridge (cf. fig. 6C) which is continuous with the malapophyses (fig. 6B). The malapophyses present a compound paralaterodorsal protuberance (fig. 6A; B: *RX*), which was named pseudorutellum by Akimov (1979) and rutellum by Griffiths (1977). The rutellar nature of the protuberance is not proved. I have not been able to discern a root, nor an actinopilinous central core. The position of the protuberance on the malapophyses (paralaterodorsal) differs from that of a rutellum (which is terminal).

Chelicera. — The chelicera consists of two segments: the body of the chelicera and the apotele (figs. 4C, 5, 6D). A cheliceral trochanter is not discernable. The anterior part of the body of the chelicera (the fixed jaw) and the apotele (the movable jaw) constitute the chela; both jaws present several more or less obtuse teeth. A voluminous ventral oncophysis (fig. 6D: *opv*) is present at the articulation between body of chelicera and apotele. The paraxial face of the chelicera (fig. 5) presents a seta and a small protuberance. The cheliceral sheath is attached to the body of the chelicera; the part posteriorly of the line of attachment (fig. 6D) is internal. The cheliceral sheath (fig. 4C: *CX.C*) is inserted on the cheliceral frame.

Legs. — All legs consist of six segments: trochanter, femur, genu, tibia, tarsus, and apotele (fig. 7). The numerical aspects of leg chaetotaxy can be represented by the following formulae (in which the number of setae of each leg is enumerated for trochanter, femur, genu, tibia, tarsus, and apotele, respectively): leg I (1-1-2-2-13-1), leg II (1-1-2-2-12-1), leg III (1-0-1-1-10-1), leg IV (0-1-0-1-10-1). All legs are monodactyl (the single unguis is represented by the last number in the formulae). Solenidia can be present on genu, tibia and tarsus, respectively; the solenidial formulae are: leg I (2-1-3), leg II (1-1-1), leg III (1-1-0), leg IV (0-1-0). The setae of the tarsus (fig. 8) represent the so-called fundamental setae: they are all of larval origin (as will be demonstrated in the paragraph on the postembryonic development). The homology of the famulus (ϵ), the proral (*p*), ungual (*u*) and subungual (*s*) setae is evident. The remaining setae certainly represent (*ft*), (*tc*), (*a*) and *pv*. Difficulties arise in the case of the anterodorsal setae, which are here indicated with the sigla *tc'*, *tc''* and *ft''*; it is possible that the notations of the last-mentioned two setae must be interchanged. The case of *Rhizoglyphus* is a simple one, and the case of *Forcellinia*, studied by Grandjean, presented more difficulties. Grandjean (1953: 393) supposed that his setae *aa* and *ba* (Grandjean, 1939: 55-60, figs. 1-2) could represent the primilateral setae. The chaetotaxy of *Rhizoglyphus* demonstrates that *aa* represents *a''*, and that *ba* represents *ft'*. In leg IV of the male (fig. 9A), *ft''* and *tc''* are replaced by suckers. In the heteromorphic male (fig. 9D), leg III has been the subject of important transformations: the segments are higher and shorter, and tarsus and apotele constitute one segment with reduced chaetotaxy. In com-

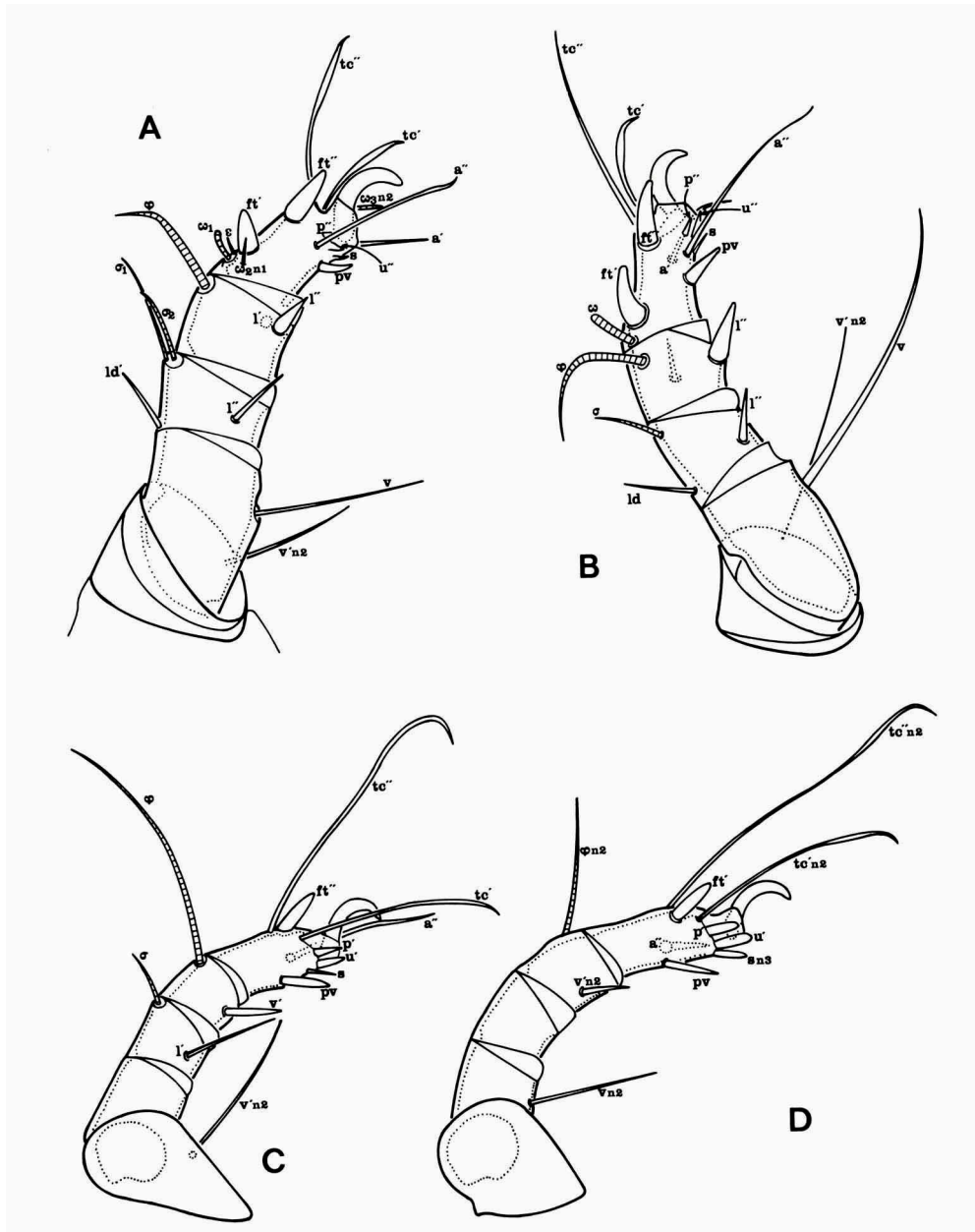


Fig. 7. *Rhizoglyphus echinopus* (Fumouze & Robin), legs of adult female, lateral (antiaxial) view; A, right leg I; B, right leg II; C, left leg III; D, left leg IV; A-D, $\times 295$.

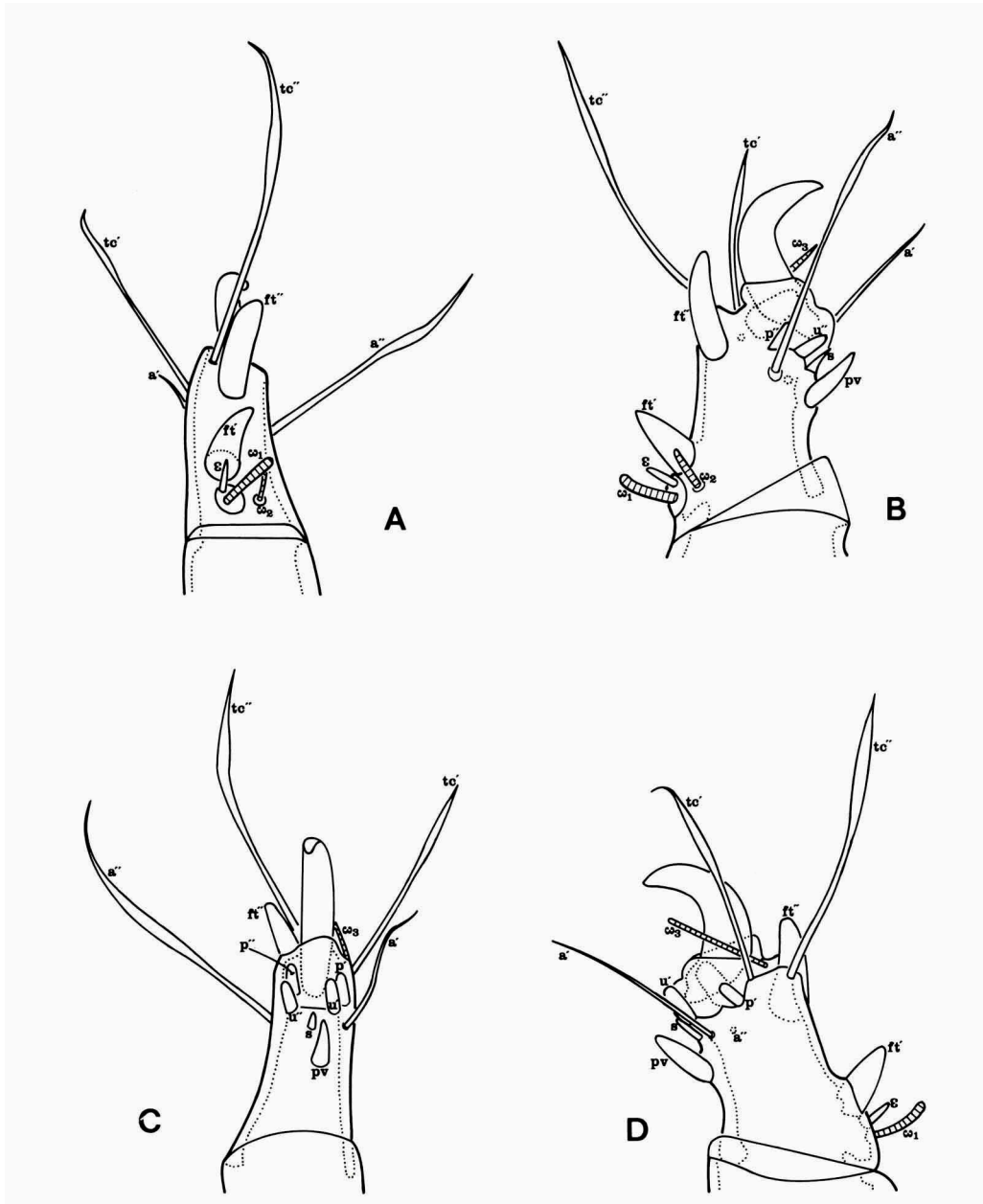


Fig. 8. *Rhizoglyphus echinopus* (Fumouze & Robin), terminal part of right leg I of adult female; A, dorsal view; B, lateral (antiaxial) view; C, ventral view; D, lateral (paraxial) view; A-D, $\times 550$.

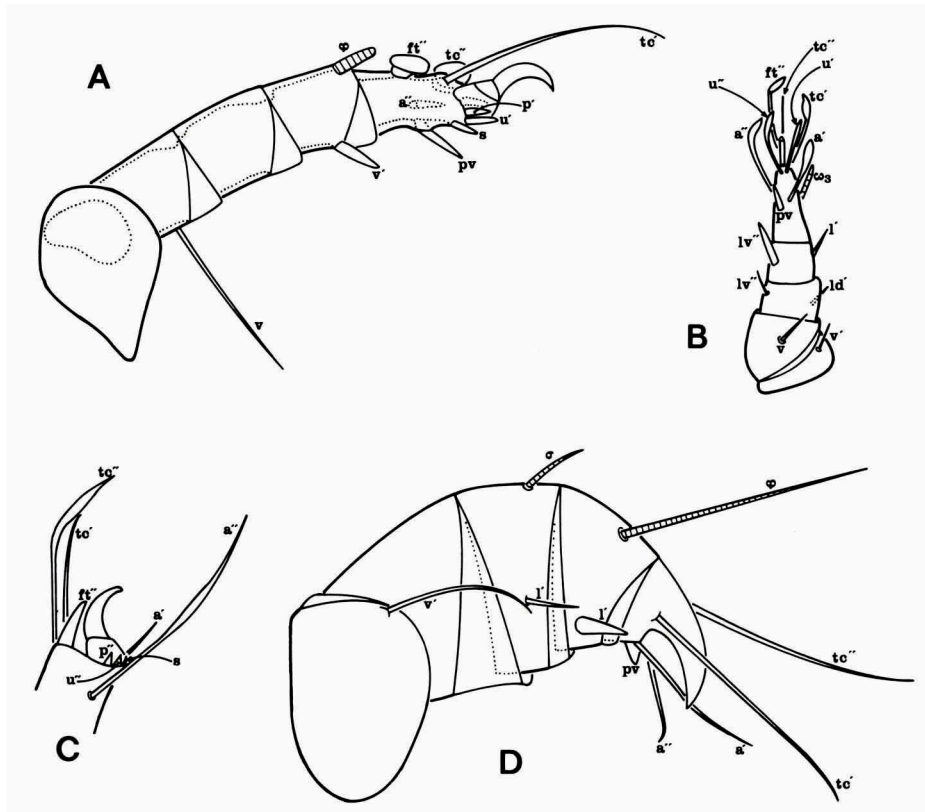


Fig. 9. *Rhizoglyphus echinopus* (Fumouze & Robin). A, left leg IV of homomorphic male, lateral (antiaxial) view; B, right leg I of hypopus, ventral view; C, terminal part of right leg II of heteromorphic male, lateral (antiaxial) view; D, left leg III of heteromorphic male, lateral (antiaxial) view; A-D, $\times 295$.

parison with tarsus III of the homomorphic male (fig. 9C), the proral, ungual and subungual setae have disappeared. The claw-like terminal part could represent the fastigial seta ft'' , the apotelic claw, or a fusion of both (possibly together with (p) , (u) and (s)).

Postembryonic development. — The life-cycle of *Rhizoglyphus* is characterized by the presence of five stases: larva, protonymph, deutonymph, tritonymph and adult. A prelarva is not known. The deutonymph has been the subject of regression; it has become an elattostase (hypopus). The elattostasic regression at the level of the deutonymph is an example of metelattosis (cf. Van der Hammen, 1975: 378; 1978: 52, 56; 1980: 100). The postembryonic development of the paraproctal region (fig. 11) is important for the homologization of the setae, and for the recognition of the number of segments. It appears that the anus is situated in the larva in segment *XIII*, and in the protonymph (and other stases) in segment *XIV*; no segments are added in the deutonymphal, tritonymphal and

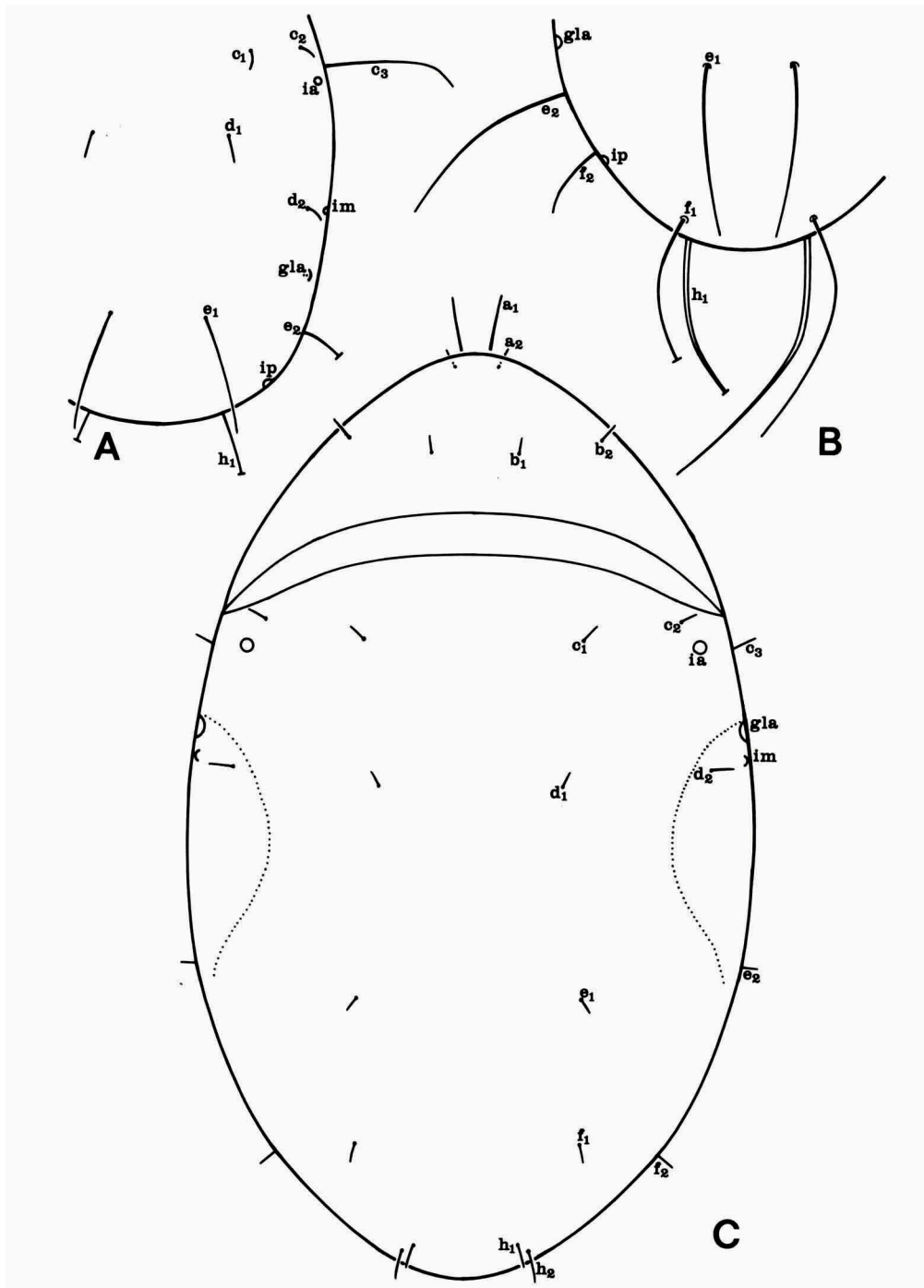


Fig. 10. *Rhizoglyphus echinopus* (Fumouze & Robin); A, opisthosoma of larva, dorsal view; B, posterior part of opisthosoma of protonymph, dorsal view; C, dorsal view of deutonymph (hypopus); A, C, $\times 268$.

adult stases (cf. Van der Hammen, 1970). In the larva (fig. 11A), the paraproctal segment (*XIII*) is glabrous (ps_1 and ps_2 are absent), whilst h_3 is also absent (suppressed, i.e. retarded by one stase). In the protonymph (fig. 11C), the paraproctal segment (*XIV*) is glabrous (ad_1 and ad_2 are absent), whilst ps_1 , ps_2 and h_3 are present. In the deutonymph (hypopus) (fig. 11D), ad_1 and ad_2 are present (they constitute suckers), whilst ps_1 , ps_2 and h_3 are replaced by suckers. In tritonymph and adult, ad_1 , ad_2 , ps_1 , ps_2 , and h_3 are all present. The case of *Rhizoglyphus* is a simple and normal example of atrichosy at two levels. In the larva (fig. 10A), two other opisthosomatic setae are lacking; evidently these are f_1 and f_2 , which appear in the protonymph (fig. 10B) and are present in deutonymph (fig. 10C), tritonymph and adult. The elattostasic regression of the deutonymph (fig. 12) pertains to the gnathosoma (which is not functional). Important deutonymphal transformations include regression in size of the notogastral setae, an advanced position of the orifice of the latero-opisthosomatic gland, a considerable development of the epimeral region, and changes in the shape of the setae of the legs (fig. 9B).

Knülle (1959: 369, figs. 22, 24-26) supposed that, in *Acarus siro* L., f_1 and f_2 are of larval origin, h_1 , h_2 , h_3 , ps_1 and ps_2 of protonymphal origin, and ad_1 and ad_2 of adult origin. Several years ago (Van der Hammen, 1969: 198), I pointed to the abnormal character of this development. It now appears that Knülle has not understood the absence of f_1 and f_2 in the larva, and probably overlooked vestiges of ad_1 and ad_2 in the nymphs.

Griffiths (1977) studied the postembryonic development of the idiosomatic setae in *Glycacarus* (Acaridida, Glycacaridae); he could not, however, study the deutonymph. His results correspond more or less with my data, although he applied a particular system of notation. His "pore" represents the (lyri)cupule *ih*. His larval seta l_5 represents h_2 ; his protonymphal setae *aP3*, *aP1* and *aP2* represent ps_1 , ps_2 and h_3 , respectively; his tritonymphal setae *aT2* and *aT1* (deutonymph not studied) represent ad_1 and ad_2 , respectively. His tritonymphal "vestige" *aT3* apparently does not represent a seta, but is included in the notation of the adult, which notation is probably not correct. He has apparently not understood the larval suppression of f_1 and f_2 .

All phaneres of the legs are larval in the case of legs I-III, and protonymphal in the case of leg IV, with exception of the following phaneres, of which the base level is mentioned between brackets (fig. 7): leg I, v' trochanter ($n2$); ω_2 ($n1$), ω_3 ($n2$); leg II, v' trochanter ($n2$); leg III, v' trochanter ($n2$); leg IV, v femur ($n2$), v' tibia ($n2$), φ ($n2$), tc' and tc'' ($n2$), s ($n3$).

AFFINITIES AND SYSTEMATIC POSITION OF ACARIDIDA

Acaridida undoubtedly represent a group of Actinotrichid mites. The chaetotaxy of idiosoma and appendages, the solenidiotaxy of the legs, and the distribution of the opisthosomatic (lyri)cupules are based on a fundamental Actinotrichid pattern. Setae present an actinopilinous core. The postembryonic

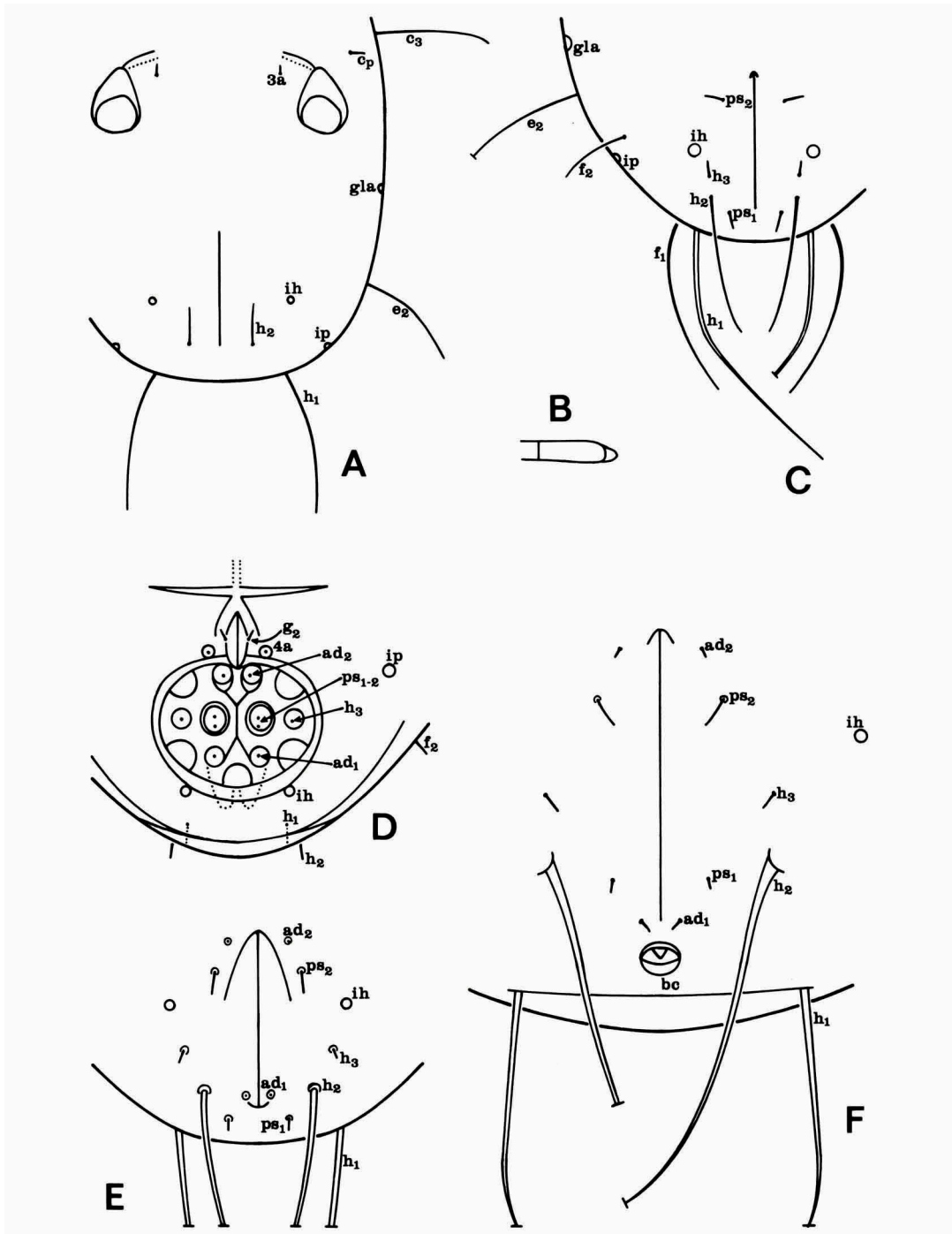


Fig. 11. *Rhizoglyphus echinopus* (Fumouze & Robin); A, B, larva; A, posterior part of idiosoma, ventral view; B, Claparède's organ, lateral view; C, posterior part of opisthosoma of protonymph, ventral view; D, anogenital region of deutonymph (hypopus), ventral view; E, posterior part of opisthosoma of tritonymph, ventral view; F, posterior part of opisthosoma of adult female, ventral view; A, C-F, $\times 268$; B, $\times 687$.

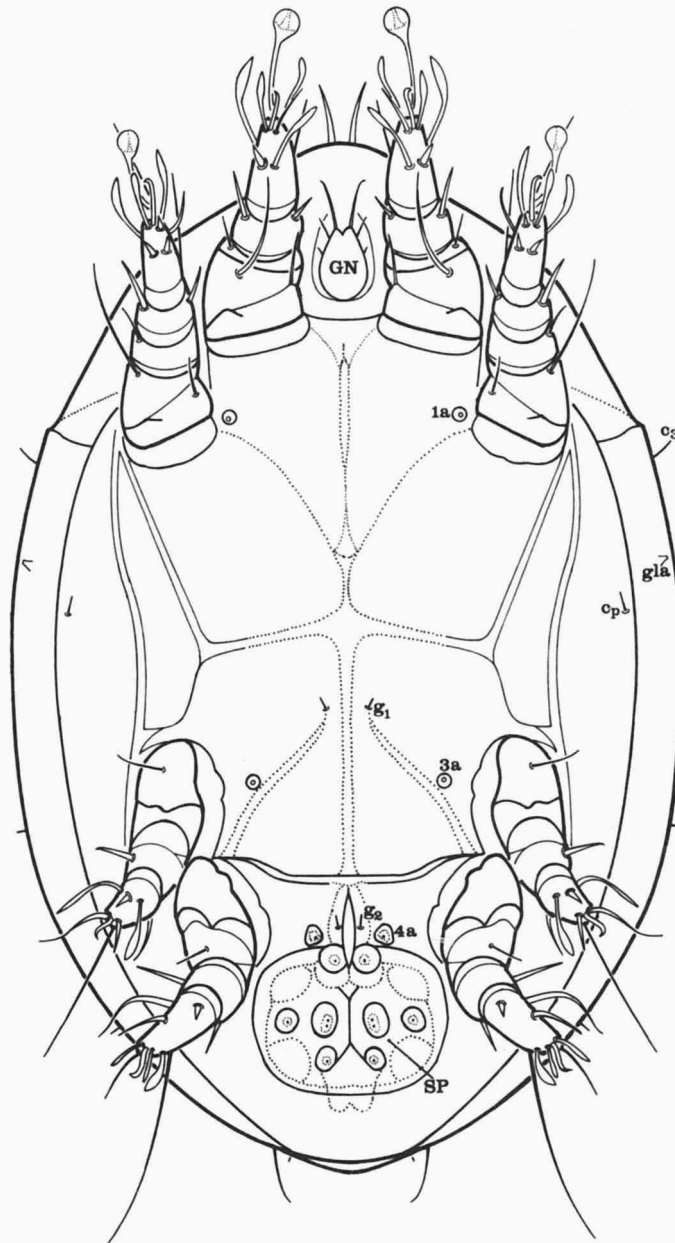


Fig. 12. *Rhizoglyphus echinopus* (Fumouze & Robin), deutonymph (hypopus), ventral view; $\times 368$.
(After Van der Hammen, 1972).

development is characterized by hysteromorphosis (the reappearance of paraproctal segments in the course of postembryonic development). There are a podocephalic canal, a trifold eugenital opening, and a sejugal furrow or interval. The ventral part of the podosoma is characterized by the presence of epimera, and the absence of coxae and sternum. The palp has no apotelic claw. Genital tracheae are known from one genus (*Gohieria*).

Acaridida are generally characterized by the following attributes (derived characters). A hypopus generally takes the place of a deutonymph. In deutonymph and male several setae are replaced by suckers. The palp has been subject to regression; the basal segments have fused with the malapophyses. Legs generally with one claw and a pulvillus. Posterior eugenital lip only partly covered by progenital lips. The paraproctal segment of the adult is constituted by segment XIV. The female generally has a bursa copulatrix. Acaridida are moreover characterized by the absence of a rostral tectum, the absence of trichobothria, the presence of a latero-opisthosomatic gland, the presence of three nymphal stases, and the external condition of the podocephalic canal.

Apart from the typical Actinotrichid characters, Acaridida share only a few characters with Oribatida, Actinedida, and Tarsonemida, respectively. The latero-opisthosomatic gland is present in most Oribatida (it is absent in several primitive groups). The immature stases of many Oribatida (particularly higher Oribatid mites) have a superficial resemblance to Acaridida (owing to the pale colour and soft tegument). In both groups, the tibial solenidia can be relatively long. According to Alberti (1980), the Acaridid sperm morphology and spermiocytogenesis present several particular, derived characters; a few primitive characters are similar to those found in a primitive family of Actinedida. The ventral structure of the podosoma in the Acaridid hypopus reminds of a similar structure in Tarsonemida; because of the great differences in sperm morphology and spermiocytogenesis, this similarity (and other similarities previously mentioned by me; cf. Van der Hammen, 1972a: 280) certainly pertain to convergence¹).

SIGLA (ABBREVIATIONS, ROMAN AND GREEK LETTERS, NUMBERS AND SYMBOLIC SIGNS)

- a*, anterior infracapitular (= genal) seta
- a*₁, *a*₂, anterior prodorsal setae (= internal and external vertical setae)
- a'* *a''*, antelateral tarsal setae
- ad*₁, *ad*₂, adanal setae
- ap.c*, capitular apodeme
- at*, line of attachment of cheliceral frame to infracapitulum

¹) The classification of Tarsonemida as a subcohort of the Eleutherengona (Actinedida) by Lindquist (1976) is not confirmed by the investigations of Alberti (1980). All four groups of Actinotrichida represent separate orders, although related to primitive Actinedida. The present state of our knowledge does not allow of a phylogenetic classification.

*b*₁, *b*₂, posterior prodorsal setae (= internal and external scapular setae)
bc, bursa copulatrix

*c*₁, *c*₂, *c*₃, *c*_p, opisthosomatic setae attributed to segments VII and VIII
CH, chelicera
cpc, podocephalic canal
CX.C, cheliceral sheath

*d*₁, *d*₂, opisthosomatic setae attributed to segment IX
ds, diachilous slit

e, supracoxal seta of palp
*e*₁, *e*₂, opisthosomatic setae attributed to segment X
eI, supracoxal seta of leg I

F, femur
*f*₁, *f*₂, opisthosomatic setae attributed to segment XI
ft', *ft''*, fastigial setae of tarsus

G, gena
*g*₁, *g*₂, genital setae
GE, genu
gla, latero-opisthosomatic gland
GN, gnathosoma
GO, Grandjean's organ

H, mentum
*h*₁, *h*₂, *h*₃, opisthosomatic setae attributed to segment XII

ia, anterior (lyri)cupule of opisthosoma
ics, superior commissural induration
ih, (lyri)cupule attributed to segment XII
im, median (lyri)cupule of opisthosoma
ip, posterior (lyri)cupule of opisthosoma

Js, superior oral commissure

l, lateral seta of legs
ld, laterodorsal seta of legs
LL, lateral lips
LS, labrum

MA, malapophysis

n1, protonymphal base level
n2, deutonymphal base level
n3, tritonymphal base level

og, eugenital opening
opv, ventral oncophysis of chelicera

p' , p'' , proral setae of tarsus

PA , palp

Pg_a , anterior genital papilla

Pg_p , posterior genital papilla

PH , pharynx

ps_1 , ps_2 , pseudanal setae

pv , primiventral seta of tarsus

PI , PII , $PIII$, PIV , legs I-IV

RX , pseudorutellum

s , subungual seta of tarsus

se , capitular saddle

SP , sucker plate

t_i , inferior tendon of apotele

t_s , superior tendon of apotele

TA , tarsus

tc' , tc'' , tectal setae of tarsus

TG , tegulum

$TR.I$, trochanter of leg I

u' , u'' , ungual setae of tarsus

v , ventral seta of legs

ϵ (epsilon), famulus

σ (sigma), σ_1 , σ_2 , solenidia of genu

φ (phi), solenidion of tibia

ω (omega), ω_1 , ω_2 , ω_3 , solenidia of tarsus

$1a$, epimeral seta of segment III

$3a$, epimeral seta of segment V

$4a$, epimeral seta of segment VI

' (prime), anterior element of the legs (paraxial in the case of legs I and II, antiaxial in the case of legs III and IV).

" (double prime), posterior element of the legs (antiaxial in the case of legs I and II, paraxial in the case of legs III and IV).

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¹⁾ The references between square brackets pertain to the Œuvres Acarologiques Complètes, 1-7, edited by L. van der Hammen (The Hague, Lochem, 1972-1976).